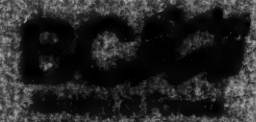
ENHANCING THE ESTABLISHMENT AND GROWTH OF ARBOREAL FORAGE LICHENS IN INTENSIVELY MANAGED FORESTS

PROBLEM ANALYSIS

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH



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ENHANCING THE ESTABLISHMENT AND GROWTH OF ARBOREAL FORAGE LICHENS IN INTENSIVELY MANAGED FORESTS

Problem Analysis

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1 INTRODUCTION

Arboreal lichens of the genera Alectoria, Bryoria, and perhaps Usnea are a major winter forage item for black-tailed deer on Vancouver Island (Cowan 1945; Gates 1968; Stevenson and Rochelle 1984). Those lichens grow in the forest canopy and are most commonly available to the deer as litterfall on the forest floor. Availability of lichen litterfall is one of several key habitat features of old-growth stands that are used by black-tailed deer as winter range.

Managers responsible for integrating intensive forestry and wildlife management on Vancouver Island seek means by which forestry practices can be used to create suitable winter habitat for black-tailed deer in second-growth stands (Nyberg 1983). The abundance of arboreal lichens in immature timber stands is characteristically low. It is the purpose of this problem analysis to explore the factors that may be acting to limit the abundance of arboreal lichens in young stands, and to identify experimental techniques and management practices that might enhance the establishment and growth of forage lichens in second growth.

2 GROWTH RATES OF LICHENS

Hypothesis: Lichen abundance in young stands is limited by the intrinsically slow growth rate of the lichens.

The growth rate of lichens is slow compared to that of many other plants; a fact that has led some observers to suspect that arboreal lichens are sparse in young forest stands because they have not had sufficient time to grow there. To evaluate this hypothesis, it is necessary to consider what is known of the growth rates of fruticose arboreal lichens, and of the factors that affect growth rates. Fruticose lichens, such as Alectoria, Bryoria, and Usnea spp. are hairlike or shrublike in growth habit. In contrast, crustose lichens form a thin crust which is closely attached to the substrate, and foliose lichens have a flattened, leaflike growth habit.

2.1 Data on Growth Rates

Growth rates of fruticose arboreal lichens have not often been measured, probably because they are more difficult to study than crustose lichens, foliose lichens, or some fruticose terrestrial lichens. Studies of linear growth rates are summarized in Table 1. Herre (1904, cited by Hale 1973) and Frey (1952, cited by Ahti 1962) studied growth rates by successively measuring lichen thalli in the field; Degelius (1964) measured thalli on twigs of known age. If the reported growth rate of 29 cm in 21 years for Alectoria (Bryoria) jubata is representative of the potential of the genus, it seems improbable that growth rates per se limit lichen abundance in young stands.

Direct measurements of changes in biomass would provide more useful information than linear measurements, but are more difficult to achieve. I am not aware of any studies in which the growth rates of arboreal fruticose lichens have been measured through successive weighing of whole thalli grown under field conditions. Culture of lichens under laboratory conditions is difficult. Growth chamber methods are complicated by the sensitivity of lichens to air pollution, their need for varying environmental conditions, and the contaminant organisms that grow on the thalli (Hale 1973). Variation in the response of individual thalli to treatments can be extreme. Pearson and Benson (1977), for example, maintained six species of arboreal lichens, including the fruticose species Evernia mesomorpha and Usnea comosa, under laboratory conditions for 12 weeks. On the average, all species lost weight under all treatments, but two specimens of Usnea comosa gained over 50% in weight.

Data on lichen abundance on trees and in stands of various ages are also relevant to evaluating the hypothesis. Detrick

TABLE 1. Linear growth rates of fruticose arboreal lichens

Species	Growth rate ($mm \cdot yr^{-1}$)	Period of study	Method	Reference
Evernia prunastri	2.0	5 yr[a]	aged substrate	Degelius 1964
Ramalina menziesii (*R. reticulata*)	30.0 (11.0 - 90.0)	7 mo	successive measurements	Herre 1904 (cited in Hale 1973, 1974)
Bryoria spp. (*Alectoria jubata*)	13.8	21 yr	successive measurements	Frey 1952 (cited in Ahti 1962)

[a]maximum age of specimen

(1984) measured lichen biomass on 121 Abies lasiocarpa in glacial basins in northern Idaho. He found an exponential relationship between lichen abundance and tree age: the curve increased gradually from approximately 20 g per tree at age 50 to 45 g per tree at age 150, then steeply to 140 g per tree at age 250. In his study area in south-central British Columbia, Antifeau (1979) reported that estimated lichen loads in stands over 100 years were appreciably higher than those in younger stands, although there was no apparent increase in lichen loads after 100 years. Mattila (1979) inventoried lichen abundance on a 4-point scale in 1083 forest stands in Finland. Although most plots that were high in lichen abundance were 120 years or older, 4.9% (five) of the 103 plots that were given the highest rating of lichen abundance were aged 61-90 years, and 1.7% (five) of the 294 plots that were rated moderate in lichen abundance were aged 31-60 years. Edmonds and Bloomfield (1984; J. Edmonds, unpubl. data) measured lichen abundance on 80 trees ranging in age from 37 to 178 years in boreal forest stands in Alberta. Their data show a general tendency for lichen abundance to increase with age, especially after about 100 years. However, the individual bearing the greatest lichen biomass was only 123 years old, and two individuals in the 75- to 85-year age range were among the highest in lichen abundance. From this limited information base, it appears that although the general pattern is that lichen abundance is great only after 100-150 years, there are instances of relatively high lichen abundance in stands aged 50-100 years.

That conclusion is consistent with my own field observations that lichens are generally sparse in stands younger than 100-150 years, but that exceptions occur. On Vancouver Island, I observed moderately high lichen abundance in a 60-year-old Douglas-fir (Pseudotsuga menziesii) stand. Clumps of Alectoria sp. up to 38 cm in length were present. Because the nearest old-growth stand was at least 0.5 km away, and no veterans were visible in the vicinity of the stand, it seems likely that the large clumps had grown from small thallus fragments, rather than having dispersed as large thalli from mature trees.

There have been a few attempts to estimate the annual production of fruticose arboreal lichen biomass. K. Simpson (unpubl. data) applied Degelius' technique of measuring lengths of lichens on twigs of known age to measuring biomass on aged branches. He determined the maximum age of 284 branches from nine Abies lasiocarpa trees, collected and weighed the Alectoria and Bryoria on each branch. Annual accumulation rates, based on linear regressions of lichen biomass (divided by branch diameter to control for variations in branch size) on branch age, ranged from 5-14%, with a mean of 8.5%. The amount of lichen on a branch is a function of

litterfall loss, litterfall gain, growth rate, and time, and growth rate is likely to vary with the position of the branch in the tree. The values reported by Simpson provide an approximation, not of growth rate, but of the rate at which lichens accumulate on branches under natural conditions.

Other authors have attempted to estimate growth rates of lichens by relating litterfall to standing crop in old-growth forests. That argument is based on the assumption that epiphyte biomass is in a state of dynamic equilibrium in old-growth forests; growth is balanced by litterfall, *in situ* decomposition, and consumption by herbivores (Pike *et al.* 1972; Rhoades 1983). Stevenson (1978a) reported litterfall rates of *Alectoria* and *Bryoria* ranging from 10.5 to 16.1% of the standing crop in old-growth forest on Vancouver Island, and assumed an intermediate growth rate of 13% of the standing crop in her calculations of carrying capacity for caribou in the Selkirk Mountains (Stevenson 1979). Figure 1 shows the theoretical growth curves of a 0.1-g lichen thallus over 40 years at some of the growth rates that have been suggested. It is apparent that small differences in percent growth rate have a large impact on change in biomass over a 40-year period.

The information that is available on growth rates of fruticose arboreal lichens is sparse. The apparent existence of some instances of relatively rapid growth indicates that the hypothesis of growth rate *per se* as the limiting factor in young stands should be rejected. However, the factors that affect growth rates should be examined.

2.2 Factors Affecting Growth Rates

The growth rate of a lichen depends on the age of the thallus and on a complex of interrelated environmental factors, including moisture, light, temperature, and nutrients.

Several models of lichen growth rates, based primarily on radial measurements of foliose and crustose thalli, have been proposed. Hale (1973) described a brief juvenile period of slow growth, a maturation period of rapid growth, and a period of maturity and senescence characterized by slow growth and thallus fragmentation. Armstrong (1976) observed a prelinear stage in which radial growth rate (but not necessarily absolute size) increased rapidly, followed by a linear stage in which growth rate was constant. He did not find evidence of a postlinear stage in which growth rate declined, although he did observe thallus fragmentation. The discrepancies between those models may have resulted from differences among lichen species, differences in environmental conditions, and differences among definitions of growth and techniques of measurement. It is not clear how models of lichen growth may

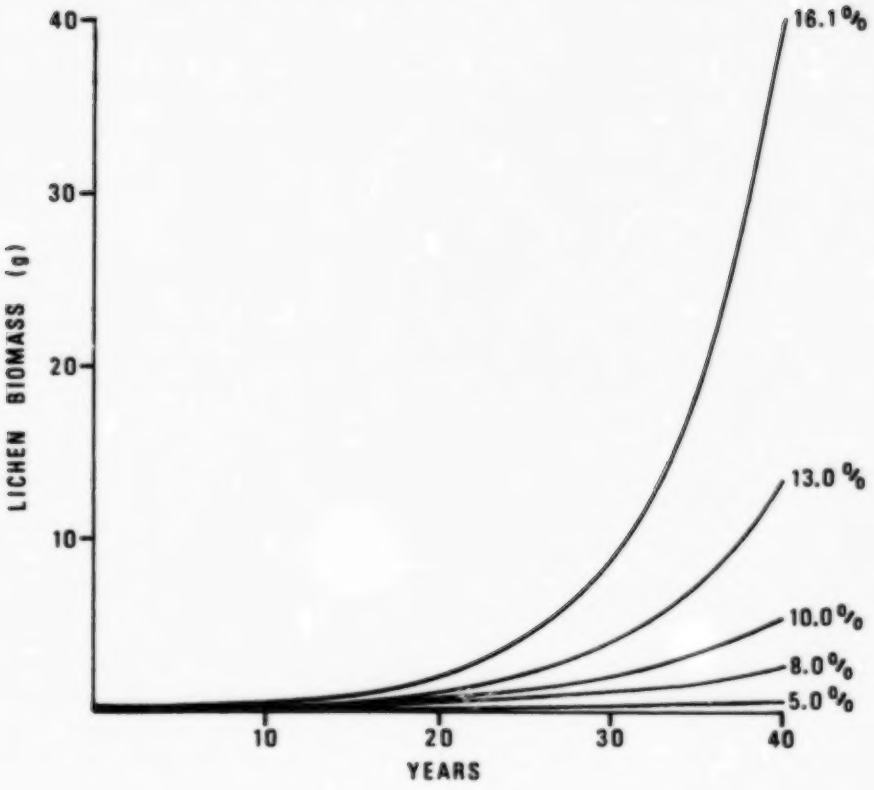

FIGURE 1. Hypothetical growth of a 0.1-g lichen thallus over 40 years at five different growth rates.

apply to fruticose arboreal lichens, but it is clear that variations in growth rate throughout the life of a thallus should be expected.

Growth takes place when a lichen thallus is wetted and metabolic activity occurs. Lichen growth has been related to a single rainstorm (Hale 1973), mean daily rainfall (Karenlampi 1971), and moisture zonation along a seashore (Hakulinen 1966, cited in Hale 1973). Humidity affects growth rates primarily by retarding water loss from wet thalli, thereby prolonging the period of metabolic activity after a rain. Furthermore, lichens have the unique capability of absorbing water vapor from the atmosphere and reaching photosynthetic levels, even when the atmosphere is not saturated (Blum 1973). Alternate wetting and drying appear to be essential to lichen growth; attempts to maintain lichens under conditions of uniform optimum humidity in the laboratory have resulted in the dissociation of the fungal and algal components of the lichen (Pearson 1970).

Light affects growth by limiting the rate of photosynthesis and ultimately the amount of assimilates available to the fungus (Hale 1973). Although the relationships between light and photosynthetic activity have been extensively studied and modelled, relationships between light and growth rates have not. Hakulinen (1966, cited in Hale 1973) reported an annual growth rate of 2.75 mm for Hypogymnia physodes growing on the south side of trees, and 2.60 mm for the same species growing on the shaded north side, but other workers have given conflicting data (Hale 1973). Studies of the response of net photosynthesis to light have shown species-specific response curves which suggest a general pattern of environmental adaptation. For example, light saturation occurs in Peltigera praetextata, a terrestrial species of closed-canopy forests, at 400 microEinsteins, whereas in Stereocaulon paschale, a terrestrial species of open woodlands, saturation occurs above 700 microEinsteins (Kershaw and Smith 1978). If other environmental conditions are held constant, it seems reasonable to expect that growth rates would increase with illuminance up to a species-specific saturation point. In nature, however, changes in light intensity are associated with changes in moisture and temperature, so that growth responses are likely to be complex.

Temperature, like light, is an environmental factor that has been studied largely in relation to photosynthetic activity and not in relation to growth rates. Optimum temperature ranges for photosynthesis vary among species (Kallio and Karenlampi 1975) and by season (Larson and Kershaw 1975). Optimal temperature ranges for photosynthesis in temperate and boreal lichens commonly fall between 10 and 25

degrees C (Kallio and Karenlampi 1975; Kershaw and Smith 1978). Thermal tolerance also varies among lichens, ranging from species capable of resistance to extreme heat and cold (Kappen 1973) to species that are quite sensitive to thermal stress (Kershaw and Smith 1978).

The nutrient supply of lichens is dissolved in water that is absorbed by the thallus. Lichens are well-known for their ability to survive in nutrient-poor environments, and to accumulate a wide range of organic and mineral nutrients (Hale 1974). Artificially increasing the nutrient supply has been shown to result in increased growth rates for several species of foliose saxicolous lichens (Hale 1973). Responses of arboreal lichens to nutrient enrichment have not been studied. On northern Vancouver Island, nutrient concentrations in Alectoria sarmentosa and Bryoria spp. were higher on nutrient-rich mature forest sites than on nutrient-poor sites, but lichen biomass was much higher in the nutrient-poor stand (S. Stevenson, unpubl. data). That observation suggests that nutrients are not limiting to the species studied, or at least that the importance of nutrient availability is overridden by other environmental conditions.

2.3 Conclusions

The information that is available on growth rates of arboreal fruticose lichens is sparse. Existing evidence, mostly indirect, suggests that growth rates adequate to result in high lichen abundance in young stands occur in nature. If high potential growth rates are not commonly realized in young stands on Vancouver Island, it may be that they are limited by environmental factors, especially moisture, light, and temperature. The hypothesis that microclimatic conditions in the young stand limit lichen abundance is examined in Section 3.

Even if the hypothesis of potential growth rate as a limiting factor is rejected, studies of growth rates would offer important benefits. Small differences in percent growth rate have a large impact on long-term biomass accumulation. Information about growth rates of lichens in relation to environmental factors would help managers make predictions about lichen development in growing stands.

3 FOREST MICROCLIMATE

Hypothesis: Lichen abundance in young stands is limited by microclimatic conditions.

Microclimatic conditions within a forest stand vary from ground level to the upper canopy, and they are generally considered to be the most important determinants of the horizontal zonation of epiphytic lichens. Microclimatic factors vary in concert, and it is often difficult to ascertain which ones exert the controlling influence on the distribution of particular lichen species. However, there is evidence that some species of lichens are very sensitive to environmental parameters, and are highly adapted to their specific environmental niche (Hosokawa *et al*. 1964; Kershaw and MacFarlane 1980). On Vancouver Island, the environmental niche most characteristically occupied by *Alectoria*, *Bryoria*, and *Usnea* spp. is the exposed canopy of mature trees. In this section, I briefly review the microclimate of the mature forest, relate the microclimatic variables to lichen biology, and postulate how the microclimatic environment for lichens may change during forest succession.

3.1 The Microclimate of Mature Forests

In a mature forest, several microclimatic zones may be differentiated. The treetop zone is the primary active surface of the forest stand. There, solar radiation is received and emitted, wind penetration occurs, temperature variation is great, dew forms on clear nights, and evaporation is strong on sunny days. The remainder of the crown area is a zone of more moderate transition between outside conditions and the relative stability of the sheltered trunk zone. The forest floor is a secondary active surface. The relative importance of the treetop zone and forest floor as active surfaces -- surfaces having the steepest microclimatic gradients -- depends on the density of the stand. Because of the sheltering influence of the forest, the climate of the forest floor is different from that of open ground.

Forest canopies are semitransparent to radiation. A dense forest canopy usually diminishes net radiation by at least an order of magnitude on clear days (Lee 1978). Photosynthesis depends on the flux density of short-wave radiant energy, within the wavelength limits of about 380-720 nm. The average irradiance at any level in a canopy is related to the irradiance above the canopy, an extinction coefficient, and the cumulative leaf area index (an index of foliage area per unit of ground) (Jarvis *et al*. 1976). In coniferous forests, which are mainly horizontal in structure, light intensity decreases sharply near the top of the canopy, and then gradually (Geiger 1966). Unfortunately, the distribution of photosynthetically useful radiant energy within a coniferous

forest canopy has not been adequately studied (Jarvis et al. 1976). An example of the relationship between leaf area index and the radiation balance (the difference between incoming and outgoing radiation fluxes) in a young spruce stand is shown in Figure 2.

In general, a forest stand acts as a moderating influence on temperature fluctuations. On sunny summer days in a dense stand, temperature is highest in the treetop zone, and several degrees cooler in the trunk area. At night, a dense stand can block the development of the kind of temperature inversions that are characteristic of open ground, so that little temperature variation occurs within the canopy. In winter, temperatures at ground level are expected to be higher than those in the canopy. However, the influence of radiation and wind on temperature profiles varies with the weather situation, and it is possible for a single stand to exhibit different types of temperature distributions on different occasions (Geiger 1966).

The relative amount of precipitation that reaches the forest floor varies greatly with the interception capacity of the canopy and with the intensity and duration of precipitation (Lee 1978). When rainfall begins, the first flurry of water stays on the needles and twigs of a closed canopy, especially if it begins gently. In the case of light rain, this initial stage may last for several hours. Evaporation occurs during every temporary letup in the rain; when precipitation resumes, the water in the canopy is replaced. If the rain continues, water begins to drip through Othe crown (Geiger 1966). It is evident that there are occasions when wetting occurs in the crown area but not at all in the trunk area, and that wetting/drying cycles are most frequent in the crown.

Dewfall, unlike rain, is almost entirely limited to the crowns of trees. Maximum deposition of dew occurs in the treetop zone; quantities at ground level under a closed stand are almost nil (Geiger 1966).

Wind speed may be reduced by 50% under an open canopy and 80% under a closed canopy (Lee 1978). Turbulence is high in the treetop zone. Wind profiles typically show a large reduction in wind speed in the crown, and a slight increase in the trunk zone. This phenomenon has been ascribed to wind penetration from gaps in the canopy (Geiger 1966), but may be the result of a horizontal pressure gradient (Jarvis et al. 1976). Wind patterns vary greatly with stand structure. Geiger (1966) showed that windspeed in and below the main canopy was much lower in an uneven-aged pine stand than in an otherwise comparable single-layered stand. McBean (1968, cited in Jarvis et al. 1976) reported that turbulence was

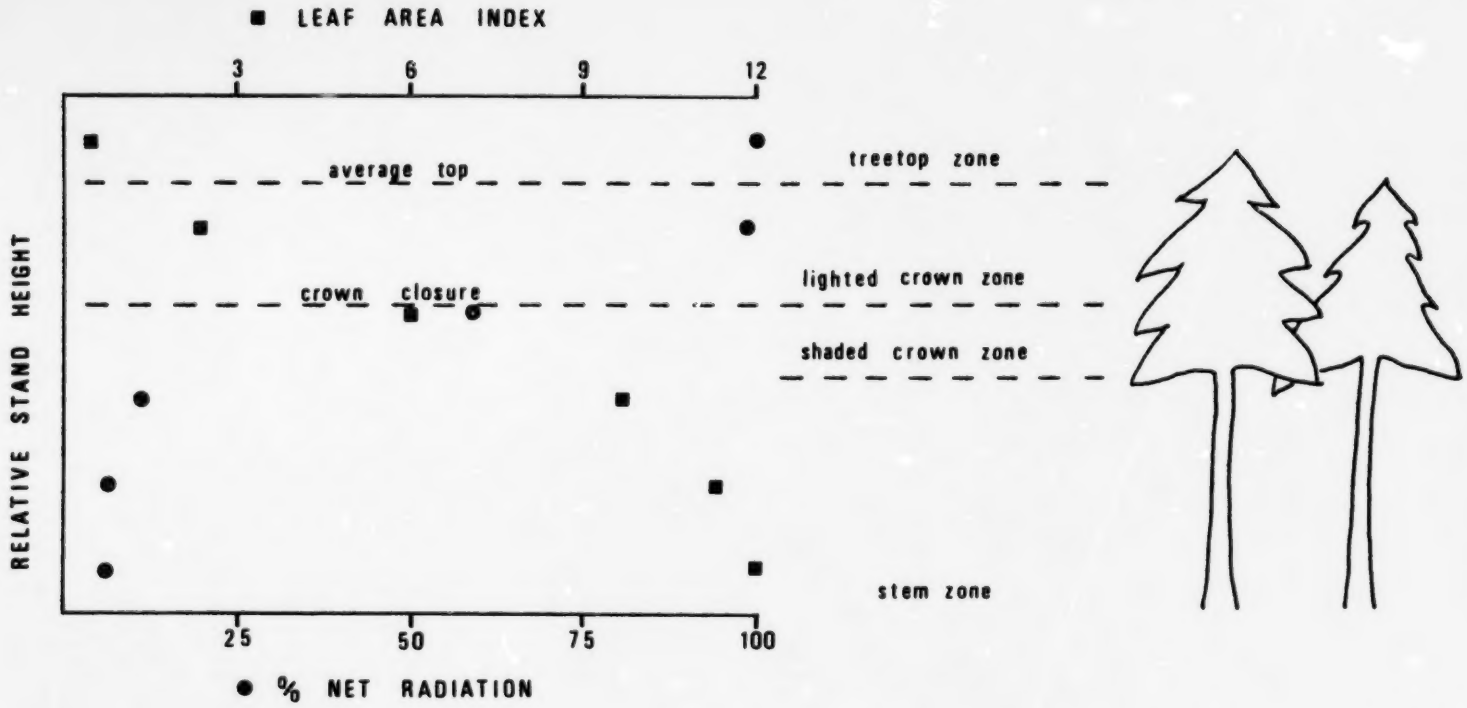

FIGURE 2. Relative stand height, cumulative leaf area index and percent net radiation (after Baumgartner 1968)

greater in a 20 m high pine stand than in a denser 5 m high pine stand.

Daytime relative humidity tends to be inversely related to temperature, decreasing with height in the forest stand (Geiger 1966; Lee 1978). Under some weather conditions, it reaches a second, smaller peak at the base of the crown (Barkman 1958; Jarvis et al. 1976), apparently due to transpiration in the canopy. Relative humidity decreases more rapidly with height in open than in dense stands (Barkman 1958).

The rate of evaporation in a forest depends on a number of factors: temperature, wind velocity, saturation deficit at the temperature of the evaporating surface, and humidity. Forests have a strong effect on evaporation, due to lower temperatures, less wind, and higher humidity than occurs in open areas (Barkman 1958). Barkman reported evaporation rates that ranged from 27% of that in the open in spruce forests to 52% in pine forests. Evaporation generally increases with height above the ground, but under some conditions it is lower at the crown base than at the tree base.

Generalized relationships between microclimatic variables and height above the ground in a coniferous stand are summarized in Table 2.

3.2 Forest Microclimate and Lichen Biology

The microclimatic requirements of lichens may be understood in terms of their twin requirements for light and water. Lichens require light for photosynthesis, but are metabolically active only when moist. Unlike vascular plants, lichen thalli do not have a stable water balance; they passively follow the fluctuations of atmospheric humidity (Blum 1973).

The horizontal zones in a forest stand offer a gradient of potential habitats for epiphytic lichens (Table 2). The tree base environment is relatively humid, protected from strong winds and temperature extremes, but receives less light and less input of liquid water. The treetop zone receives more light, precipitation, and dew, but is subject to more water loss and to extremes of temperature.

Epiphytic lichens appear to be physiologically adapted to the microclimatic zones in which they occur. Hosokawa et al. (1964) studied the light compensation point, daily compensation period, photosynthetic rate, and water relations in some epiphytic mosses and lichens. The minimum illumination intensities at which the species reached the compensation point, as well as the optimal illumination intensity, were lowest for species that ordinarily grew at the

TABLE 2. Microclimatic variables and height in a coniferous forest

Canopy position	Solar radiation	Temperature variation	Precipitation	Wind speed	Relative humidity	Evaporation
Treetop zone	H	H	H	H	L	H
Lighted crown zone	H-M	H-M	H-M	H-M	M-L	H-M
Shaded crown zone	L	L	L	L	M	L
Trunk zone	L	L	L	L-M	M	L-M
Tree base zone	L	L	L	VL	H	L

H high
M medium
L low
VL very low

base of the tree, intermediate for trunk species, and highest for crown species. The crown species were best adapted to low atmospheric humidity and to high light intensity.

It seems likely that another key microclimatic characteristic of the crown environment is variation. Pearson (1969) observed that the distribution patterns of lichens in a Minnesota bog suggested that variation of environmental conditions, especially moisture, was more important than constant optimal conditions. Pearson and Benson (1977) tested the hypothesis that lichen species that ordinarily occurred on parts of trees where humidity and temperature varied would grow better under variable laboratory conditions than species that naturally occurred where environmental conditions were more uniform. The researchers experienced methodological difficulties, and although their results tended to confirm the hypothesis, they were not conclusive.

The microclimatic environment in which most pendulous fruticose lichens occur on Vancouver Island is one of high radiation, high input of moisture, high evaporation rates, and therefore, frequent cycles of wetting and drying. In a stand of average density, those conditions prevail in the treetop and lighted crown zones (Fig. 2). In open, exposed forests those conditions prevail at lower heights in the canopy, and the lichens in question are found at lower heights on trees. They are absent or sparse under the conditions of shade, low moisture input, and low evaporation that prevail under a dense forest canopy. Szczawinski (1953) compared radiation in the open, as measured with a light meter, with radiation inside various forest associations on southern Vancouver Island. In the Gaultheria shallon - lichen association, where Alectoria and Bryoria spp. were abundant below 2 m, he measured 35-50% of the light in the open; the lichens were less abundant or absent in the associations that received less radiation. In the absence of more specific data on the ecophysiology of Alectoria, Bryoria, and Usnea spp., it seems reasonable to assume that in the climate of Vancouver Island, high radiation, high input of moisture, and high evaporation rates offer the optimum conditions for their growth.

3.3 Microclimatic Changes and Lichen Habitat in Successional Stands

The literature on forest microclimate is composed mainly of intensive studies of one or two forest stands; few researchers have focussed on the microclimatic changes that occur as stands develop. This section is based largely on inferred relationships between stand structure and microclimate, rather than on actual data. The model of forest succession used here is based on Harcombe's (1984) recommendation that features of the schemes of Thomas (1979) and Walmsley et al. (1980) be combined. The kinds of changes

in microclimate and in lichen habitat that are hypothesized during the course of stand development are summarized in Table 3.

The microclimate of a recently cleared area is more severe than that within a forest. It is not as severe as the microclimate over bare ground, unless the clearcut has been intensely burned, because of the modifying influence of the low vegetation (Geiger 1966). Solar radiation is high, maximum and minimum air temperatures are extreme, and humidity is low (Bell et al. 1974; Lee 1978). Wind speed is higher than it is under the shelter of a mature forest, though not as great as in the treetop zone, because of the general increase in wind speed with height above the ground (Geiger 1966). The lower wind speeds near the ground in the grass-forb stage may mean that its microclimate is more severe than that of the treetop zone of a mature forest, at least under some weather conditions.

In the shrub-seedling stage the canopy has not yet closed. The crowns of the young trees are exposed to light, and they still have an open-grown form. The microclimate is not as severe as it was in the grass-forb stage. Toward the end of this phase, the establishment of thallus fragments on twigs begins. Stevenson (1978b) reported that in 15- to 25-year-old stands on Vancouver Island, Bryoria thalli were approximately 3 times as abundant as Alectoria thalli, even though Alectoria was the most abundant species in adjacent stands of mature timber. Of the two genera, Bryoria generally occupies higher positions in the crowns of trees, and it may have been more abundant in the second-growth because the microclimate was more favorable for its establishment than for Alectoria.

During the pole-sapling stage, canopy closure occurs. Solar radiation below the level of canopy closure is much reduced, and the lower branches of the trees begin to die back. In one of the few studies of microclimate in relation to stand development, Mitscherlich (1940, cited in Geiger 1976) measured light intensity at the forest floor in 87 fir stands (Fig. 3). In his study, canopy closure occurred after about 17 years, and light intensity dropped abruptly to about 10% of that in the open. Once canopy closure has occurred, the lower portions of the canopy develop a microclimate similar to that of the crown base in older stands (Table 2). That microclimate is unsuitable for the Bryoria fragments and probably also the Alectoria fragments that established themselves during the shrub-seedling stage. The process of establishment continues, but branches are quickly overtopped and shaded, so that they become unsuitable for further lichen development unless the stand is opened.

TABLE 3. Microclimatic changes and lichen habitat in successional stands

Successional stage	Typical age range (yrs)	Stand structure	Microclimatic	Forage lichens
Grass - forb	0-5	Seedlings established through planting or natural regeneration	Severe; high solar radiation, extreme temperatures, low humidity, moderate wind speed	Absent except on residuals
Shrub-seedling	5-15	Canopy has not closed; young trees have open-grown form	Severe microclimate of grass - forb stage increasingly moderated by vegetation	Establishment of thallus fragments on twigs begins
Pole-sapling	15-25	Canopy closure occurs Dieback of lower branches begins	Solar radiation much reduced below level of canopy closure	Establishment of thallus fragments continues, but light levels may be too low for lichens in lower canopy
Young seral	25-40	Continued dieback of lower branches; natural thinning begins	Microclimatic zones characteristic of mature stand are present	Usually very sparse. In exposed stands, may be moderately abundant in upper crown and trunk area
Maturing seral	40-140	Natural thinning has affected stand structure; a regeneration layer is present	As in Table 2. Natural thinning results in increased light penetration to lower canopy	Approach levels of maximum abundance on optimum sites by the end of the stage
Overmature seral/ mature climax	140+	Seral species in main canopy begin dying and are replaced by regeneration	As in Table 2	Level of abundance stabilizes

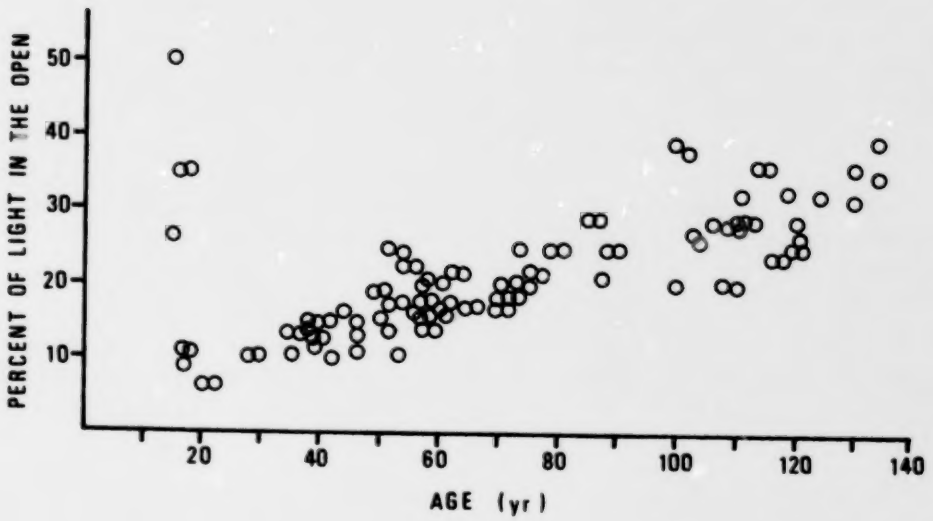

FIGURE 3. Relation between the age of a stand of fir and the light penetrating to the forest floor (after Mitscherlich, cited in Geiger 1966, p. 301).

At the young seral stage, the process of natural thinning begins. Dieback of lower branches continues, and the microclimatic conditions of a trunk zone develop. The microclimatic pattern characteristic of a mature stand (Table 2) is complete. Figure 3 suggests that light penetration has increased from the pole-sapling stage, but according to Barkman (1958), the data on which it is based were for cultivated plantations, and light intensity in natural forests would continue to decrease. Lichen abundance remains very low in most young seral stands, but is moderate in some exposed, south-facing stands. I have collected lichen clumps of up to 32 cm in a xeric 40-year-old stand that was distant from any dispersal source, which indicates that enough time had elapsed for considerable growth to take place. In those young seral stands in which significant amounts of lichen are present, the zones of greatest lichen abundance appear to be the lighted crown zone (but not the young branch tips of the treetop zone) and the dead or dying branches of the trunk zone. That distribution pattern may occur because of higher evaporation rates in the trunk zone, or it may be that the stand structure allows more light to penetrate to the trunk zone than into the shaded crown zone.

At this stage in stand development, the opportunity exists to experimentally manipulate stand structure to encourage lichen development through precommercial thinning. Because the objective is to thin the stand enough that light penetration to the crown and trunk area is increased for an extended period of time, spacing should be wider or thinning more frequent than what is ordinarily prescribed for silvicultural purposes. This is also the first period in stand development during which artificial dispersal of lichen fragments is likely to be effective in increasing long-term lichen abundance (Section 5).

In a maturing seral stand, natural thinning has affected stand structure, and a regeneration layer is present. The presence of a regeneration layer is indicative of increased light levels reaching the forest floor; light in the canopy is also increased. In time, the regeneration layer itself begins to affect the microclimate in the lower part of the stand. It intercepts radiation and precipitation, increases humidity, and lowers wind speed and evaporation. Lichen development approaches or attains the potential of the site by the end of this period. As the stand grows, lichen associations gradually extend upward in the tree canopy. Commercial thinnings early in this stage could be used experimentally to increase lichen production by letting more light into the canopy.

At the overmature seral and mature climax stages, the seral species in the main canopy begin to die and are replaced

by regeneration. The microclimate is as described in Section 3.1. Lichen abundance reaches the potential of the site and stabilizes.

It seems likely that two microclimatic factors limit the development of lichens on otherwise favorable sites during the pole-sapling, young seral, and maturing seral stages. The first is that from the time canopy closure occurs until natural thinning allows increased light penetration, the microclimate is too shady and lacks the frequent wetting/drying cycles that the lichens are believed to require. The second is that even where those conditions exist in young stands -- in the exposed crowns -- the growth rate of the trees is often so rapid that the branches having a suitable microclimate are soon overtopped, shaded and protected by the growth of the tree above them. The first problem can be met by the precommercial and commercial thinning suggested above. The second problem is more difficult, in that the thinning regimes are likely to increase the growth rates of the trees and accelerate microclimatic change. Very wide spacing or repeated lighter thinnings is suggested in order to increase the light penetrating the canopy enough to compensate for the increased shading from above.

3.4 Conclusions

Microclimatic conditions in a forest stand vary from ground level to the upper canopy. Epiphytes that characteristically occupy a particular height zone in the forest are physiologically adapted to the microclimatic conditions of that zone. On Vancouver Island, most species of Alectoria, Bryoria and Usnea characteristically occur in the upper canopy and exposed crowns of mature trees. They are found in lower positions in more open stands. In the upper canopy and exposed crown, solar radiation, moisture input, wind speeds, and evaporation rates are high, relative humidity is low, and temperature variations are extreme. It is likely that for lichens, the combination of high light levels and frequent wetting/drying cycles are the key characteristics of the exposed crown habitat.

In immature stands, microclimatic changes occur as stand structure changes. From the time canopy closure occurs until natural thinning allows increased light penetration, the microclimate in most of the canopy is too shady and lacks frequent wetting/drying cycles. Even in the exposed crowns of young stands, the branches that offer a suitable microclimate are soon overtopped by the rapidly growing trees.

To determine whether lichen development can be accelerated by altering microclimatic conditions, experimental precommercial thinning to very wide spacing at the young seral stage is recommended.

4 SUBSTRATE CHARACTERISTICS

Hypothesis: Lichen abundance in young stands is limited by the substrate characteristics of young trees.

Lichens vary in the degree to which they are restricted to certain substrates. Some corticolous species are so substrate-specific that they are found only on a single species of tree or shrub, whereas others occur on rock and soil as well as bark. As a general rule, the most substrate-specific species are those in closest contact with the substrate (Brodo 1973). Compared to many corticolous species, Alectorioid lichens are relatively substrate-indifferent. Their most common substrates are coniferous trees and deciduous trees with similar bark characteristics, such as birch. It is not clear whether the lichens select those trees because of their bark characteristics, or whether they require the climate and general environment of coniferous forests, and simply occupy the most available substrate. As a wide variety of trees within each forest type are used as substrates, the latter possibility seems most likely (Brodo and Hawksworth 1977).

Bark characteristics of trees change with age. The purpose of this section is to evaluate those age-related changes in relation to texture, water relations, and chemistry -- the properties that are most important to lichens (Brodo 1973) -- and to assess the likelihood that bark characteristics of young trees limit the establishment and development of fruticose lichens.

4.1 Bark Texture

The texture of the bark surface changes with the age of the tree. In some genera, such as Abies, the cork cambium of the first-formed periderm remains functional for many years, resulting in the smooth external features of the bark, even at maturity (Zimmermann and Brown 1971). But in most species, the first periderm dies and is replaced by new periderms which develop in the underlying tissue of the bark. In many genera, such as Tsuga and Pinus, these periderms have the shape of overlapping concave scales. As the cork produced by each new periderm matures, the outer layers become cut off from the underlying living tissue, and die. They are exfoliated in small pieces, which reflect the organization of the successive periderms (Morey 1973). Thus, the bark surface typically changes from smooth-textured and stable to rough-textured and unstable, but in a manner and at a rate that is species-specific.

Bark texture can affect the ease of colonization, and the type of lichen most likely to colonize. Smooth bark surfaces commonly support communities of crustose lichens, whereas

fruticose lichens occur most abundantly on rough surfaces (Degelius 1964; Kalgutkar and Bird 1969). Compared to crustose and foliose lichens, fruticose lichens are late immigrants. Degelius (1964) found that Alectoria (Bryoria) jubata occurred on twigs of ash (Fraxinus)\that were 12 or more years old, but that the fruticose lichen community in general was better developed on older branches. On trunks of larch (Larix) and pine (Pinus), the appearance of fruticose lichens coincided with tree age 50 (Kalgutkar and Bird 1969). However, succession on branches proceeds more rapidly than succession on the trunk (Degelius 1964; Kalgutkar and Bird 1969). Yarranton (1972) observed a high incidence of Alectoria (Bryoria) nadvornikiana on young (20-40 year) twigs of black spruce (Picea mariana). Stevenson (1978b) reported colonization of 2-year-old twigs of Douglas-fir by small fragments of Alectoria sarmentosa and Bryoria spp. Evidently, the bark of young trees is able to support fruticose lichens in the branch systems, though the slower rate of succession on trunks may be related to bark texture.

Once a tree is old enough to produce new periderms, a process is initiated that results in the scaling of the outer layers of bark. According to Barkman (1958), the rate of exfoliation is greatest on rapidly growing trees, on trunks with large unbranched sections, and on the sunny side of the trunk. Instability of the bark can be a factor in limiting lichen abundance. Yarranton (1972) observed scaling below the live crown of black spruce, but little scaling within the crown itself, and speculated that scaling was a factor in the reduced lichen abundance on the older parts of the tree. It is possible that rapidly growing individuals of species that exfoliate readily, such as Douglas-fir, could experience reduced lichen abundance on the trunk. It seems less likely that bark scaling would limit lichen abundance within the canopy, where thallus fragments are commonly entwined around twigs and needles.

4.2 Water Relations

The moisture-holding capacity of bark has been related by some authors to the general epiphyte vegetation. The relationship is most significant under xeric conditions (Brodo 1973). It seems likely that foliose and crustose species would be more strongly affected by bark moisture than fruticose species. Kalgutkar and Bird (1969) found that the water-holding capacity of white-barked pine was greater than that of alpine larch, but that the larch supported more fruticose lichens. Bark samples from pines aged 60-259 and larches aged 53-286 revealed no apparent relationship between tree age and the moisture-holding capacity of the bark. Although there is little evidence for any conclusion, it seems unlikely that differences in moisture-holding capacity between the bark of young and old trees can account for differences in

the abundance of lichens that are not in close contact with their substrate.

4.3 Bark Chemistry

Lichens derive their mineral nutrition from nutrients dissolved in the water with which they come in contact. The nutrients are deposited on the lichens through dustfall and absorbed when the thallus is wetted. They are present in rainfall and are augmented by leaching as the rain drips through the tree canopy. Bossermann and Hagner (1981) showed that for pendulous fruticose lichens, such as Usnea, rainfall is a more important source of elements than dustfall.

I am not aware of studies comparing the nutrient composition of bark, of throughfall precipitation, or of arboreal lichens in coniferous stands of different ages. However, there is some evidence that the nutrient composition of arboreal lichens is related to their position in the canopy, presumably due to the effects of throughfall precipitation. Solberg (1979) found that the concentration of seven elements (N, P, S, Se, V, Hg, and U) averaged 15% greater in Alectoria (Bryoria) fremontii growing at 1.5-2.5 m than at 4-5 m in Pinus sylvestris. Similar observations have been made on Vancouver Island (S. Stevenson, unpubl. data). If nutrient concentrations in arboreal lichens are related to the biomass of foliage above them, as those reports suggest, then nutrient concentrations of lichens in young stands could be expected to be lower than in old stands because of the relatively lower canopy biomass.

The hydrogen ion concentration, as well as the nutrient composition, of the water is important, as the ability of the lichens to absorb elements is affected by the pH of the water in which they are dissolved (Brodo 1973). Little information is available on relationships between stand age and pH of bark or of throughfall precipitation. Margot (1965, cited in Brodo 1973) reported significant differences in the pH of the stem flow with age in Populus, but Kalgutkar and Bird (1969) found no age-related differences in the pH of bark samples from Pinus and Larix.

Although changes in the elemental composition of throughfall precipitation with stand age are likely, and changes in pH may occur, those changes do not necessarily affect lichen abundance. Stevenson (1978a) found that Alectoria sarmentosa and Bryoria spp. were more abundant on nutrient-poor sites on upper slopes than on nutrient-rich sites on lower slopes, and that they were generally more abundant in the upper than lower portions of the canopy. Those observations do not support the hypothesis that Alectoria sarmentosa and Bryoria spp. are limited by nutrients.

4.4 Conclusions

All lichens exhibit substrate preferences to some degree, although fruticose arboreal lichens are not typically high in substrate specificity. Because substrate characteristics of trees change with age, the hypothesis that they might limit lichen abundance in young stands was examined. Smoothness of the bark surface may slow colonization by fruticose lichens on very young twigs of some species, and on the trunk, but probably not on branch parts aged 20 years or more. Rapid exfoliation of the bark may limit lichen abundance on the lower bole of fast-growing trees, but probably not in the branch systems. Changes in the moisture-holding capacity of the bark with age are probably a factor of minor importance, at least on Vancouver Island. Availability of nutrients to arboreal lichens probably does increase with stand age, but observed patterns of lichen distribution do not support the hypothesis that nutrient availability is a limiting factor.

5 DISPERSAL

Hypothesis: Lichen abundance in young stands is limited by the dispersal ability of propagules.

For lichens to establish themselves in young forests, viable propagules must be liberated from the parent plants, transported into the young stand, deposited, and attached to the new substrate. The purpose of this section is to review the biology of dispersal in fruticose arboreal lichens, and to assess the likelihood that their abundance in second-growth stands is limited by distance from a dispersal source.

5.1 Propagules

Lichens produce several types of reproductive propagules. Ascospores are sexual propagules of the fungal component of the lichen synthesis. They range in size from 1 to 510 microns, but are normally closer to the small end of that scale. For a lichen thallus to be produced through sexual reproduction, an ascospore must germinate and recombine with an appropriate alga. This process is assumed to occur frequently in nature, although it has not actually been observed (Bailey 1976). However, it is not the dominant mode of reproduction for the pendulous fruticose lichens in question. Spore-producing structures (apothecia) are rare or absent in 15 of the 21 arboreal species of Alectoria and Bryoria in British Columbia, and also in some species of Usnea.

Lichens also produce vegetative propagules, which incorporate the fungal-algal symbiosis. Soredia are clumps of a few algal cells enveloped by fungal hyphae which erupt through pores or cracks in the cortex of the thallus. The diameter of individual soredia ranges from 25 to 100 microns, but soredia sometimes adhere to one another, forming a sub-macroscopic mass (Hale 1974). There is considerable indirect evidence that species that produce soredia have an advantage in dispersal over species that do not (Hale 1974; Bailey 1976; Stevenson 1978b). However, they are normally present only in six species of arboreal Alectoria and Bryoria in British Columbia, and in several species of Usnea.

Many lichen species produce isidia -- cylindrical protuberances of the upper cortex containing both algal and fungal tissues -- which are easily broken off and are thought to function as propagules. Isidia are larger than soredia, ranging from 0.01 to 0.3 mm in diameter and from 0.5 to 3.0 mm in length (Hale 1974). True isidia do not occur in the genera Alectoria or Bryoria, but isidioid branches and spinules, which probably function as propagules, are present in some species. True isidia are present in some species of Usnea.

Probably the most important method of dispersal for most pendulous fruticose lichens, at least on a local scale, is the production of erratics, or detached thallus fragments which continue independent growth. While studying litterfall in coniferous forests on northern Vancouver Island (Stevenson 1978a), I noted that minute fragments of Alectoria sarmentosa and Bryoria spp. were ubiquitous in litterfall traps, and common on the surface of a day-old snowpack. In a study of dispersal of Alectorioid lichens into regenerating forests (Stevenson 1978b), I attempted to distinguish on the basis of growth habit between thalli that had originated from fragments and thalli that had originated from a point source - either soredia or spores. Of 211 thalli examined on 2-year-old twigs, all appeared to have originated from thallus fragments rather than from soredia or spores. When I examined twigs up to 14 years old, I was able to find a few thalli that could have originated from spores or soredia, although thallus fragments were dominant on the older twigs as well. These observations indicate the importance of thallus fragments as propagules, but they do not necessarily imply that smaller propagules are not important, especially on older substrates or over greater distances.

5.2 Processes of Dispersal and Establishment

The stages of dispersal of lichen propagules include liberation from the parent thallus, transport to and deposition on a suitable substrate, and germination or attachment to that substrate (Bailey 1976).

Wind, water, and animals are potential agents of liberation and transport for all propagule types, and active liberation of spores also occurs. For pendulous arboreal lichens, wind is undoubtedly the most important agent for both liberation and transport. In some cases, the ability of wind to liberate propagules is related to the water content of the thalli. In several lichen species studied by Bailey (1966), wet thalli exposed to wind liberated more soredia than did dry thalli. Von Schrenk (1898) found that wet thalli of Usnea spp. were about 3 times heavier than dry thalli, had only about 25% as much tensile strength, and liberated thallus fragments at lower wind velocities than did dry thalli. This evidence suggests that windstorms accompanied by rain are probably the optimum conditions for the dispersal of pendulous arboreal lichens.

Wind is generally considered to be the pre-eminent agent for the large-scale transport of lichen propagules over long distances (Barkman 1958; Bailey 1976). Spores believed to be referable to lichen species, soredia, and thallus fragments have all been found in traps sampling the air spora (Bailey 1976). There is an inverse relationship between propagule size and airborne transport distance; spores are believed to

be best adapted for long-distance dispersal by wind, soredia for medium-distance dispersal, and thallus fragments for local dispersal (Barkman 1958). However, almost nothing is known of the quantitative values of those dispersal distances.

Deposition of airborne fragments takes place by any of three modes: sedimentation under gravity, wash-out by precipitation, and impaction upon surfaces (Gregory 1973). Wind-tunnel experiments demonstrated that large spores impact more efficiently against obstructions than small spores (Gregory 1973). If this relationship applies to larger, irregular objects then thallus fragments may be better suited than soredia and soredia than spores to impaction on twigs and branches.

Two principal modes of attachment occur in Usnea, Alectoria and Bryoria. Von Schrenk (1898) observed that within a few weeks, filaments of Usnea become tangled among the stems and needles of conifers. The tangling is due to the coiling and uncoiling of the filaments as they are alternately wetted and dried, a phenomenon that occurs also in Alectoria and Bryoria. The second mode of attachment is the formation of hapters -- filaments that become attached to the substrate by means of hyphae (Hawksworth 1972). Many of the fragments of Alectoria sarmentosa and Bryoria spp. which I observed on the twigs of young trees on Vancouver Island (Stevenson 1978b) had attached themselves by means of one or more hapters. Apparently a similar phenomenon occurs in species of Usnea (Bailey 1976). Hapters develop quickly; I noted instances of hapter formation on 1-year-old twigs of Tsuga heterophylla.

Spores, soredia, isidia, and thallus fragments are all potential particles of dispersal in the genera Alectoria, Bryoria, and Usnea. Wind is probably the most important means of liberation and transport of propagules. The importance of thallus fragments in local dispersal is apparent. Thallus fragments are not generally considered a means of long distance dispersal, but several species exist in which apothecia, soredia and isidia are absent or very rare. The importance of spores or soredia, in species that do produce them, is unclear. In short, thallus fragments are known to accomplish local dispersal, but the importance of other propagules in local or long-distance dispersal is unknown for the genera in question. The next section examines the question of whether dispersal opportunities might limit the occurrence or abundance of Alectoria, Bryoria, and Usnea.

5.3 Dispersal Distance and Lichen Abundance

A body of literature exists on the dispersal of elements of the air spora, such as spores, bacteria, and pollen, and of macroscopic objects such as seeds and insects (Gregory 1973; Wolfenbarger 1975), but most of this information is difficult

to relate to dispersal of lichen propagules. Because size and shape are important determinants of dispersal distances, it is inappropriate to try to predict the effective range of dispersal of thallus fragments or soredia from studies carried out on different kinds of organisms. Furthermore, dispersal studies have tended to concentrate on short-range movement. Experimental study of dispersal over a few kilometres is almost non-existent, and experts do not agree on its probable magnitude (Gregory 1973).

The literature is not helpful in predicting effective dispersal distances of lichen propagules, but it does provide some generalized information on shapes of dispersal curves. Wolfenbarger (1975) presented an idealized graph based on relative amounts of pollen falling at various distances. He described three zones which he considered characteristic of many or most curves of organism dispersal, such as the two illustrated in Figure 4. In the local zone numbers of organisms decrease rapidly as distance from the local source increases. The extralocal zone occurs as a sharp turn in the regression curve. In the regional zone the curve tends to parallel the abscissa. That part of a dispersal curve derives from the regional vegetation (Wolfenbarger 1975), or from the tails of the distributions of many sources too for away to show a gradient (Gregory 1973). The magnitude of those escape fractions increases with decreased particle size, greater liberation height, and increased turbulence.

Stevenson (1978b) studied abundance of Alectorioid lichen thalli in young (15-24 yr) coniferous forests in relation to distance from the adjacent mature timber. Numbers of thallus fragments found on the sample twigs decreased as distance from the timber edge increased (Fig. 5). The curve defined by these points appears to have the same form as the generalized curve for organism dispersal shown in Figure 4. Numbers of thallus fragments in the regional zone do not appear to taper off with increasing distance from the mature timber. If, as Gregory (1973) suggests, the distal portion of the curve represents dispersal from many sources, then this amount of dispersal may be general in the area.

Two important questions are suggested by that study. First, is the level of lichen abundance that was observed in the regional zone adequate to establish a new lichen community; would additional input of thallus fragments lead to greater lichen abundance in the developing stand? Second, would the level of lichen abundance observed in the regional zone also be found where the overall area of mature forest was greatly reduced, as in the center of a large burn? Conditions like that will occur with increasing frequency as more and more forested areas are managed for timber production.

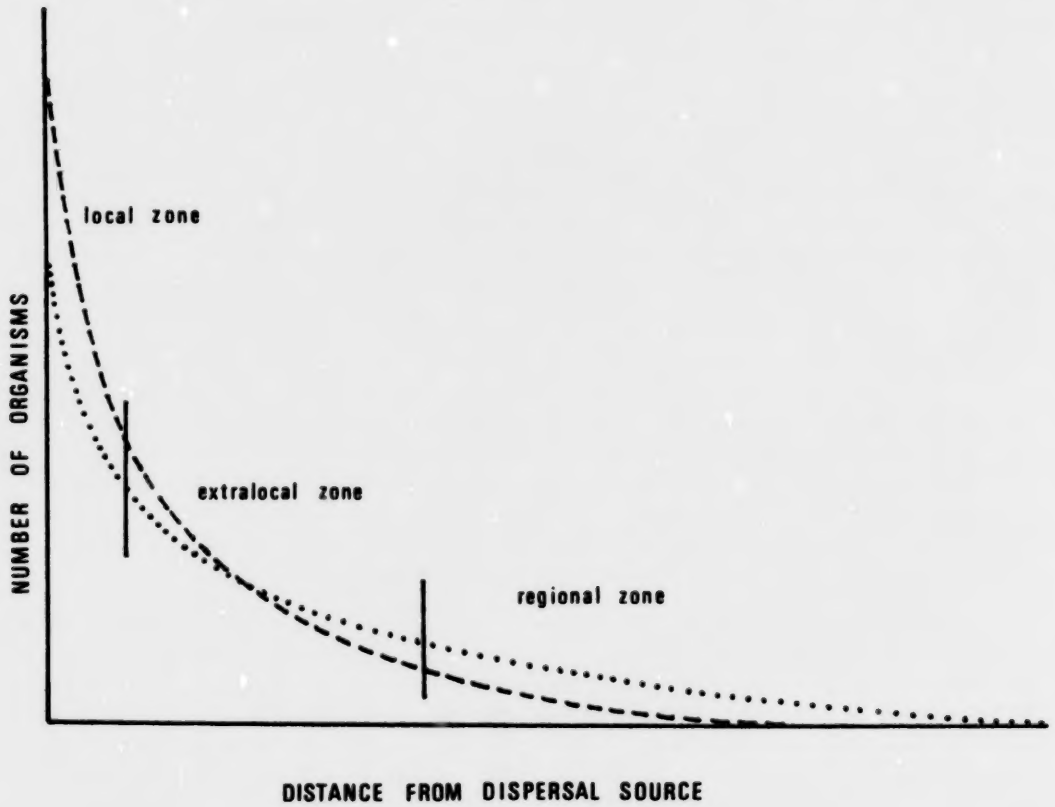

FIGURE 4. Trends in regression curves of organism dispersal (Wolfenbarger 1975, p. 9).

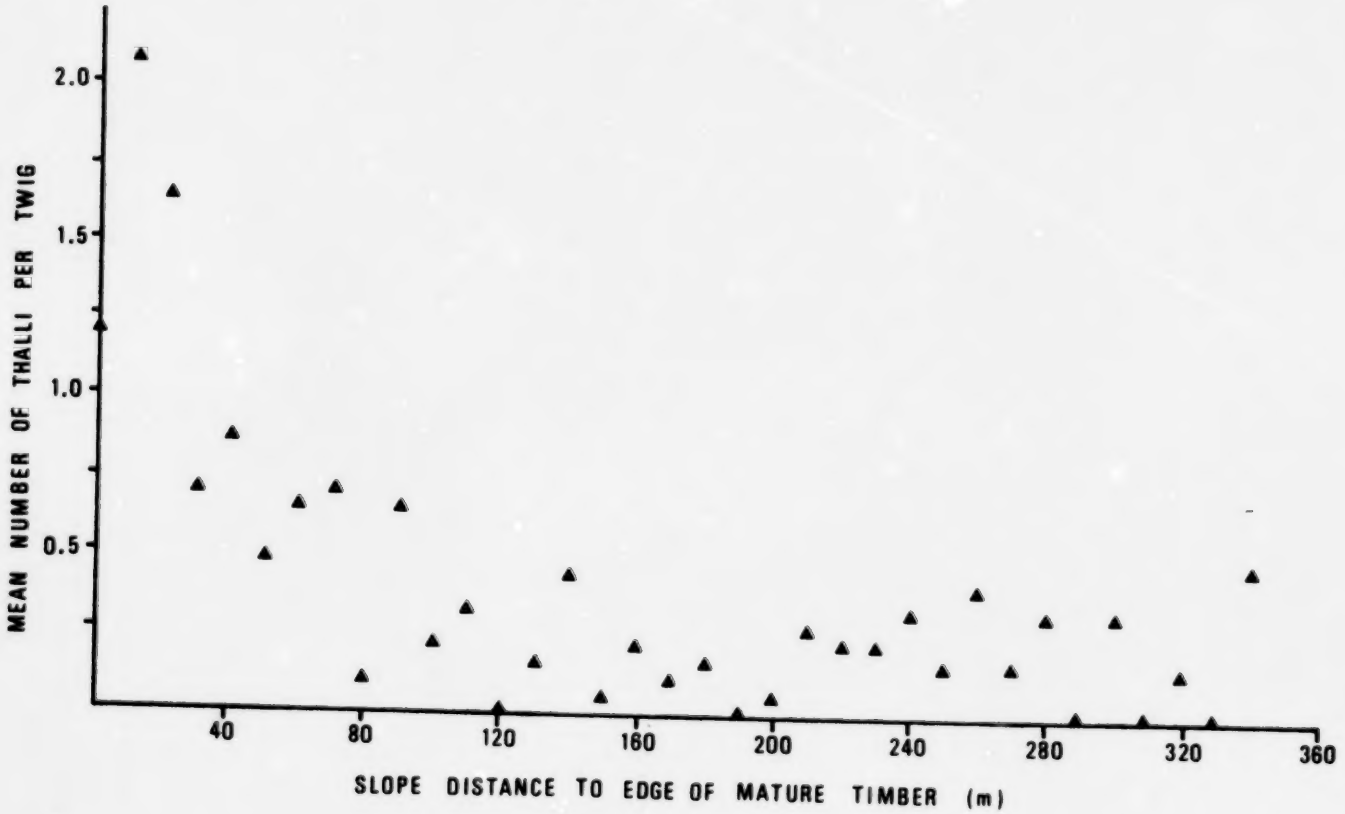

FIGURE 5. Thallus fragments of Alectoria and Bryoria on 2-year-old twigs in second growth and distance from mature timber (Stevenson 1978b).

There is ample evidence that where old-growth timber is isolated in small islands, as in Great Britain, some lichen species are restricted to those very old woodlands (Rose 1976). There is also some evidence that inability to colonize distant habitats may have been a factor in limiting the distribution of the restricted species. Stevenson (1978*b*) compared the species identified by Rose as limited to very old hardwood stands with species that were common and general in occurrence, and found that the two groups differed significantly ($p<0.01$) in their dispersal mechanisms: old forest species were more likely to have spore-producing structures, and common and general species were more likely to have soredia or isidia. In Great Britain, at least four of the eight arboreal species of *Alectoria* and *Bryoria* are restricted to old-growth forests. It is unclear to what extent they are restricted because of microclimatic unsuitability of the younger stands, and to what extent they are restricted because of inability to colonize at a distance.

In summer 1984, I visited second-growth stands on Vancouver Island to observe patterns of lichen abundance in regenerating forests. In the Cowichan and Shawnigan areas, where extensive patch logging has taken place, lichens appear to have recolonized suitable stands of second growth, regardless of the proximity of mature timber. In contrast, in the Sayward Forest, where 30 148 ha of timbered land burned in 1938 (J. Parminter, pers. comm.), lichen distribution appeared to be more strongly controlled by proximity to residual timber. These informal observations suggest that where the proportion of mature to immature timber is low, the background level of dispersal of lichen propagules is lower than it is where there are still large areas of mature timber.

5.4 Conclusions

In the genera *Alectoria*, *Bryoria*, and *Usnea*, four types of propagule are potentially important in dispersal: spores, soredia, isidia, and thallus fragments. All species are capable of producing thallus fragments, but only some species produce any of the other propagule types. Liberation and transport of thallus fragments through wind action appears to be the dominant means of local dispersal of pendulous arboreal lichens. It is unclear to what distance dispersal of thallus fragments is effective. Even less is known of the roles of the other propagules in the dispersal of those lichens.

At the level of patch logging that is common today on Vancouver Island, as in the Nimpkish Valley, there appears to be a background level of dispersal through thallus fragmentation that is ubiquitous. As more and more of the forested land on the Island is managed for intensive timber production, old-growth forests will become habitat islands in a matrix of young managed stands. Under those conditions,

will that background level of dispersal be maintained? That question could be investigated by comparing dispersal in areas of patch logging with dispersal in a large area of second-growth forest, such as the Sayward Forest.

A second important question is whether artificial augmentation of the background level of dispersal would result in a long-lasting increase in lichen abundance in second-growth stands. It seems reasonable to expect that where intraspecific competition is clearly not limiting, and the microclimate is suitable for growth, increased abundance of propagules would result in increased abundance of lichens. This question can only be answered through experimentation. A widely spaced stand at the young seral stage, in a location that is suitable for lichen growth, should offer good conditions for the experiment.

6 SUMMARY AND CONCLUSIONS

The objectives of the problem analysis were to explore the factors that potentially limit the abundance of Alectoria, Bryoria, and Usnea in young stands, and to identify experimental techniques and management practices that might enhance the establishment and growth of forage lichens in second-growth forests. Hypotheses concerning the importance of lichen growth rates, microclimate in young stands, substrate characteristics of young trees, and the dispersal ability of lichens were examined.

Indirect evidence indicates that growth rates adequate to result in high lichen abundance in young stands occur in nature. The hypothesis that lichen abundance in young stands is limited by the intrinsically slow growth rates of the lichens was rejected.

Small differences in percent growth rate have a large impact on long-term biomass accumulation. Research on growth rates of lichens in relation to environmental factors would help managers make predictions about lichen development in growing stands.

On Vancouver Island, most Alectoria, Bryoria, and Usnea species characteristically occur in the upper canopy and exposed crowns of mature trees. In open stands, they are found in lower positions. It is likely that the lichens are physiologically adapted to high solar radiation and frequent wetting/drying cycles.

From the time canopy closure occurs in immature stands until natural thinning allows increased light penetration, the microclimate in most of the canopy is shady and lacks frequent wetting/drying cycles. Even in the exposed crowns of young stands, the branches that offer a suitable microclimate are soon overtopped by the rapidly growing trees.

To determine whether lichen development can be accelerated by altering microclimatic conditions, experimental precommercial thinning to very wide spacing at the young seral stage is recommended.

The little evidence that is available does not support the hypothesis that substrate characteristics -- bark texture, moisture-holding capacity, or chemistry -- of young trees limit lichen abundance, at least not in parts of the canopy more than 20 years old.

Liberation and transport of thallus fragments through wind action appears to be the dominant means of local dispersal of Alectoria, Bryoria, and Usnea. The effective distance of that

dispersal mechanism is unknown. The roles of other propagules in the dispersal of those lichens are unknown.

The hypothesis that dispersal ability limits, or potentially limits, lichen abundance in young stands could not be rejected. It is unknown whether background levels of dispersal adequate to propagate lichens at their present levels will be maintained as old-growth forests become habitat islands in a matrix of young managed stands. Comparative studies of dispersal in areas having different ratios of old to young growth are recommended.

Regardless of the relationship between old growth and the background level of dispersal, it is possible that lichen development could be accelerated in some second-growth stands through artificial augmentation of dispersal. It is hypothesized that in stands having a suitable microclimate (either naturally or through special management), increased input of thallus fragments would result in increased lichen abundance. Experimental testing of this hypothesis is recommended.

Research activities are proposed in four broad areas:

1. studies of growth rates in relation to microclimatic conditions;
2. comparative assessments of background levels of dispersal;
3. artificial augmentation of dispersal; and
4. experimental manipulation of stand structure to improve microclimatic conditions for lichens.

Those activities should be carried out, not as isolated projects, but as part of a coordinated program with the long-term goal of understanding the processes of lichen dispersal, establishment, and growth, and their relationships to the forest. Such an understanding would allow the lichen/forest ecosystem to be modelled and managed.

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